Model simulation of changes in N_2O and NO emissions with conversion of tropical rain forests to pastures in the Costa Rican Atlantic Zone

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Abstract. Nitrous oxide (N₂O) and nitric oxide (NO) are among the trace gases of concern because of their importance in global climate and atmospheric chemistry. Modeling techniques are needed for simulating the spatial and temporal dynamics of N₂O and NO emissions from soils into the atmosphere. In this study, we modified the ecosystem model CENTURY to simulate changes in N₂O and NO soil emissions through the process of converting tropical moist forests to pastures in the Atlantic Lowlands of Costa Rica. Measurements of water-filled pore space (WFPS) and fluxes of N₂O and NO from a chronosequence of pastures were used for calibration and testing of the model. It was found that the N₂O+NO — WFPS and N₂O:NO — WFPS relationships as developed from primary forests could be generalized to the chronosequence of pastures and other land use systems in the region. Modeled net increases (compared to primary forests) in total N₂O and NO production after conversion from forest to pasture were 514 kg N ha⁻¹ during the first 15 years under normal field conditions. The nitrogen loss in the form of N₂O and NO during the first 15 years could range from 401 to 548 kg N ha⁻¹, depending on the amounts of forest residue remaining on pasture sites. N₂O-N accounted for 90% of the gas fluxes, while NO-N accounted for 10%. Sensitivity analysis indicated that the impacts of forest-pasture conversion on N₂O and NO emissions from soil into the atmosphere were complex, depending on the initial conditions of the forest-derived pastures, management practices, soil physical and chemical conditions and their changes over time, N availability, and climate. It is therefore important to incorporate the spatial and temporal heterogeneities of those controlling factors in estimating regional and global N₂O and NO emissions from soils into the atmosphere.

1. Introduction

Deforestation in tropical areas has been extensive during the last 3 decades. Deforested lands are often converted to cattle pastures, agricultural crop lands, and shifting agriculture to support millions of people in this region and for commodity export. These changing land use patterns are of concern with respect to loss of biodiversity [e.g., *Lugo et al.*, 1993; *Lugo*, 1995; *Phillips*, 1997] and alterations of global biogeochemical cycles [e.g., *Keller et al.*, 1997]. One consequence of land use changes in the tropics and elsewhere is the net change in trace gas fluxes to the atmosphere.

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Paper number 1999GB900002. 0886-6236/99/1999GB900002\$12.00 which have important implications for the regulation of Earth's radiative balance and the maintenance of the oxidizing capacity of the atmosphere [Keller et al., 1997].

Nitrous oxide is an important "greenhouse" gas with a lifetime of about 150 years in the troposphere. It ultimately is destroyed by photolysis in the stratosphere, where it also plays an important role in the balance of stratospheric ozone [Crutzen, 1970; McElroy and McConnell, 1971; Prinn et al., 1990]. Nitric oxide, on the other hand, is a highly reactive species that contributes to increasing lower tropospheric ozone concentrations.

Tropical forest soils are estimated to be the single largest global source of N_2O , accounting for 3 Tg N_2O -N of a total global budget of approximately 14 Tg [Keller and Matson, 1994; Bouwman et al., 1995; Nevison and Holland, 1997]. Those estimates are based on crude, simple extrapolation techniques that take very few environmental controls into account. Therefore it is important to improve the estimation of N_2O emissions at the regional and global scales by incorporating land use, soil, and climatic factors. As

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part of an effort to scale up N_2O and NO emission rates from sites to regions where changes in land use have been so dramatic, we have adapted CENTURY, an ecosystem level model with emphasis on soil organic matter and nutrient (N, S, and P) cycling [Parton et al., 1987, 1994a; Schimel et al., 1997], to simulate N_2O and NO emissions for the dominant land use types of the Costa Rican Caribbean lowlands (S. Liu et al., Simulation of nitrous oxide and nitric oxide emissions from tropical primary forests in the Costa Rican Atlantic Zone, submitted to Environmental Modelling and Software, 1999) (hereinafter referred to as submitted manuscript, 1999). The objective of the work described in this paper is to adapt CENTURY for simulation of N_2O and NO emissions dynamics through the process of forest conversion to pasture and subsequent pasture aging in the Costa Rican Caribbean lowlands.

2. Methods

2.1. Study Area

Field measurements of water-filled pore space (WFPS) and soil-atmosphere fluxes of N₂O and NO were collected from seven actively grazed forest-derived pastures near Guacimo, Costa Rica (10°12'N, 83°32'W). No climate observations were available from this area during the observation period. However, regional distribution of annual rainfall and temperature indicated that the climate was very similar to that at the La Selva Biological Station (10°26'N, 84°00'W), where records of monthly precipitation and maximum and minimum temperatures for the measurement period were available (Liu et al., submitted manuscript, 1999). Therefore the climate data from La Selva were used in this study.

The pastures, aged 2, 3, 5, 10, 12, 18, and 25 years, were sampled eight times during the period February to November 1992 [Keller et al., 1993]. Eight measurements of N₂O flux and four measurements of NO flux were made per sampling at each site. All cleared sites had been immediately set to pasture after deforestation, except for the 18-year-old site, which was cultivated for 1 year. The soils underlying all of these pastures were classified as Humitropepts. Soil bulk densities and porosities at these sites are listed in Table 1. This chronosequence of pastures was resampled in 1996 [Veldkamp et al., 1999]. The 12- and 25-year-old pastures that were sampled in 1992 were not resampled because they had been converted into other forms of agriculture. A 3-year-old pasture, converted from the forest site of 1992

Table 1. Soil Bulk Densities and Porosities of Pastures at Different Ages near Guacimo, Costa Rica

Pasture Age, years	Bulk Density, g cm ⁻³	Porosity
2	0.67	0.71
3	0.78	0.69
5	0.83	0.69
10	0.82	0.68
12	0.8	0.70
18	0.98	0.63
25	0.79	0.70

Bulk density measurements were taken from 0-5 cm soil depth. Porosity is 1 - (bulk density)/(particle density). Particle density was 2.65 g cm³, estimated from *Reiners et al.*[1994].

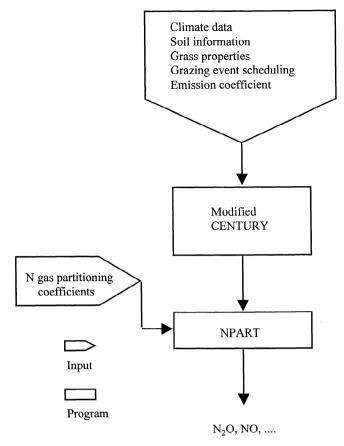


Figure 1. The structure of the modified CENTURY model used for the simulation of N_2O and NO emissions from a chronosequence of pastures. See text for details.

[Keller et al., 1993], was also resampled by Veldkamp et al. [1999].

The dynamics of soil organic carbon (SOC) after forest-pasture conversion was illustrated with two independent sets of field measurements in the same area [Reiners et al., 1994; Veldkamp, 1994]. Veldkamp [1994] measured SOC contents at a primary forest and four pastures aged 2, 5, 10, and 18 years old, to investigate the SOC dynamics after forest clearing. At approximately the same time, Reiners et al. [1994] studied the SOC differences among different land uses, for which three primary forest sites and three active pastures, aged about 20-31, 20-31, and 36 years, were investigated. For consistency, we converted SOC contents [Reiners et al., 1994] into total SOC (g C m⁻²), using the following formula [Veldkamp, 1994]:

$$SOC = C_s L \rho_b \times 100 \tag{1}$$

where C_s is soil carbon content (kg C kg⁻¹ soil), L is soil layer thickness (m), and ρ_b is soil bulk density (Mg m⁻³). The impact of cattle trampling on the SOC calculation was considered, following the procedure of *Veldkamp* [1994].

2.2. Model Structure

CENTURY simulates C, N, P, and S cycles in various ecosystems, including pastures, forests, crops, and savannas, with the capability of modeling the impacts of management practices

(e.g., fertilization, cultivation, irrigation) and natural disturbances such as fire and hurricane [Parton et al., 1987, 1994a]. The monthly time step version of the model was used in this study. We have modified the hydrologic submodel and the N_2O and NO production submodel to simulate N_2O and NO emissions from primary rain forests in Costa Rica (Liu et al., submitted manuscript, 1999). The modified CENTURY was then used here to simulate N_2O and NO emissions from the chronosequence of pastures (Figure 1). The postprocessor Nitrogen PARTitioning (NPART) of the modified CENTURY partitions the total simulated nitrogen trace emission rates into N_2O and NO fluxes based on the simulated WFPS and the N_2O and NO partitioning coefficients described in section 2.4.

2.3. Model Parameterization

Most of the values describing the initial conditions of the site (Table 2) are the same as values used for the primary moist forest simulation (Liu et al., submitted manuscript, 1999). However, with conversion to pasture, compaction increased soil bulk density from 0.70 to 0.80 g cm³ [Keller et al., 1993; Reiners et al., 1994]. We assumed that all the sites in the chronosequence had experienced slash and burn before being sown into grass, a

Table 2. Initial Values for the Pasture Newly Converted From a Primary Rain Forest

Variable	Initial Value	References	
Soil, 0-3	30 cm Depth	1	
Sand content	0.12	Liu et al. (1999)	
Silt content	0.15	Liu et al. (1999)	
Clay content	0.73	Liu et al. (1999)	
pH	4.5	Liu et al. (1999)	
Soil C, g C m ⁻²	5560	Liu et al. (1999)	
SOM C/N ratio	10	Liu et al. (1999)	
	Grass		
Potential aboveground production, gC m ⁻² y ⁻¹	1800	Veldkamp [1993]	
Fraction of C allocated to roots	0.115	Veldkamp [1993]	
Shoot C:N ratio	45:1	Ibrahim [1994]	
Root C:N ratio	55:1	Parton et al. [1993]	
Root death rate, month-1	0.042	Veldkamp [1993]	
Lignin content in shoot, %	20	Parton et al. [1993]	
Lignin content in roots, %	26	Parton et al. [1993]	
G_{i}	razing ^a		
Fraction of live shoots removed by grazing	0.3		
Fraction of standing dead removed by grazing	0.15		
Fraction of consumed C which is excreted in feces	0.3		
Fraction of consumed N which is excreted	0.8		
Lignin content of feces	0.25		

Table is based on Liu et al. (Submitted manuscript, 1999). Organic matter addition, in the form of ash, wood, and roots, is listed in Table 3.

aValues are based on field observation (B.A.M. Bouman, personal communication, 1998).

common practice in this area [Keller et al., 1997], and that 10% of C and N was lost from the top 30 cm soil layer owing to burning as observed by Ewel et al. [1981] in the top 3 cm soil layer. Within the model, forest residues (ash, wood, coarse roots and fine roots) (Table 3) were added to the derived pasture in the first 3 months of the pasture establishment. We also assumed that grazing was withheld in the first 6 months to promote pasture establishment.

Atmospheric deposition of nitrogen was added according to field measurements obtained for La Selva Biological Station [Eklund et al., 1997]. Potential net primary productivity of the pastures was set at 190 g C m⁻² month⁻¹ [Veldkamp, 1993]. Fertilizer had not been applied to these sites [Keller et al., 1997]. Grazing intensity was set to 30% of the net shoot primary production and 15% of the dead standing biomass, with 30% of C and 80% of N returning to the site in the form of urine and feces (Table 2).

2.4. Generalization of the Primary Forest N_2O and NO Submodel

Our forest N_2O and NO submodel was based on field measurements obtained from three primary rain forests at La Selva Biological Station, Costa Rica (Liu et al., submitted manuscript, 1999). In that submodel, the combined fluxes of N_2O and NO $(N_{\rm N2O+NO})$, in g N m⁻² month⁻¹) were simulated as a function of gross N mineralized $(N_{\rm min.}$ in g N m⁻² month⁻¹) and WFPS:

$$N_{\text{N2O+NO}} = a N_{min} F_f \tag{2}$$

where a is the emission coefficient of the soil and F_f is the scaling factor of WFPS (W_f or WFPS of the forest soil) on the combined fluxes of N_2O and NO and is described by

$$F_f = 0.00085 \ e^{9.13Wf} \tag{3}$$

when $W_f < 0.77$. If $W_f \ge 0.77$, then $F_f = 1$.

The ratio of N_2O to NO was used to partition N_2O from NO in the combined fluxes as a function of W_t in the rain forest:

$$(N_2O:NO)_f = 4.9 \times 10^{-6} e^{20.56 Wf}$$
 (4)

where $(N_2O:NO)_f$ is the $N_2O:NO$ ratio in rain forests.

The observed combined fluxes of N_2O and NO varied greatly among forest-derived pastures [Keller et al., 1993]. While we could find a set of relationships describing NN2O+NO — W_p (WFPS measured at pasture sites) and $N_2O:NO$ — W_p for each site based on field measurements, it is difficult to extrapolate those relationships to other sites in the same area. We generalized the partitioning relationships developed from rain forest (Liu et al., submitted manuscript, 1999) to represent the diverse relationships found in the chronosequence of pastures in the same area using a scaling technique:

$$F_p = 0.00085 \ e^{9.13 \ (Wp + \text{shift1})} \tag{5}$$

or

$$F_p = 0.00085 \ C e^{9.13 \ Wp} \quad \text{with } C = e^{\text{shift1}}$$
 (6)

where shift1 is the necessary translation of W_p measured in the pasture in order to use the forest $N_2O+NO-W_f$ relationship to predict $N_2O+NO-W_p$ at the pasture site. Shift1 really corresponds to a scaling factor C to the whole relationship (see (6)). In order to determine the size of the translation shift1 or the scaling factor C, the SAS nonlinear regression (NLIN) procedure

Table 3. Impact of Organic Matter Addition to the Site From Clear-cutting, Slash and Burn on N_2O and NO Emissions of Forest-Derived Pastures

	Low	Normal	High	C:N ratio
	Organi	ic Matter Addition	, gC m ⁻²	
Ash	168 ^a	350 ^h	525	17°
Branch	715	1022°	1329	111°
Large wood	574	820°	1066	263°
Coarse roots	1774	2534°	3296	178
Fine roots	72ª	347°	520	31°
	Net Incred	use in N_2O and NC	D Emissions ^d	
N_2O	360	463	494	
	(16)	(16)	(18)	
NO	41	51	54	
	(11)	(12)	(13)	

^a Values are from Ewel et al. [1981].

[SAS Institute Inc., 1990] was used. First, the combined measured fluxes of N_2O and NO from the pastures were normalized by the maximum flux observed at each corresponding site during the study period. Then the normalized N_2O and NO field measurements and their corresponding W_p were used for the optimization of shift1 at each site. Agreements between the measured and predicted (based on (6) and the optimized shift1) $N_2O+NO-W_p$ relationships found in these pastures (Figures 2 and 3) indicated that the $N_2O+NO-W_p$ relationship we developed for the rain forests could be generalized to pastures in the same area. This generality should not be interpreted in the absolute sense, because a scaling factor for the relationship between combined trace gas fluxes and W_p has been added to represent the shift of the predicted fluxes along the WFPS axis.

By the same process, we found that the relationship between the ratio of N_2O and NO and W_f as developed from the primary rain forest (see (3)) could also be generalized to pastures at different ages (Figure 4). The generalized equation is

$$(N_2O:NO)_p = 4.9 \times 10^{-6} e^{20.56 (W_f + \text{shift2})}$$
 (7)

where $(N_2O:NO)_p$ is the $N_2O:NO$ ratio at the pasture sites and shift2 is the necessary translation of W_p measured in the pasture in order to use the forest $(N_2O:NO)_f - W_f$ relationship to predict $(N_2O:NO)_p - W_p$ at the pasture site.

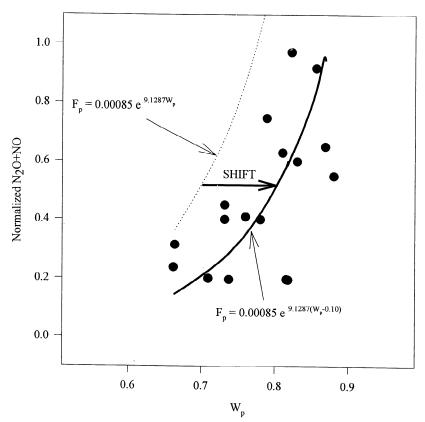


Figure 2. Comparison between the predicted and measured relationships between the combined normalized N_2O+NO fluxes and water filled pore space (WFPS) W_ρ at a 20-year-old pasture. The predictions (lines) were based on the N_2O+NO — WFPS relationship developed from rain forest (Liu et al., submitted manuscript, 1999) with or without the shift1 factor. N_2O and NO fluxes were normalized by the maximum flux. In this case, the scaling factor shift1 was -0.10.

^b Estimate is based on stand total biomass (Liu et al., submitted manuscript, 1999) and *Ewel et al.* [1981].

^c Values are based on Liu et al.(submitted manuscript, 1999).

 $^{^{\}rm d}$ Numbers in parentheses are the number of years with net increase of N_2O or NO

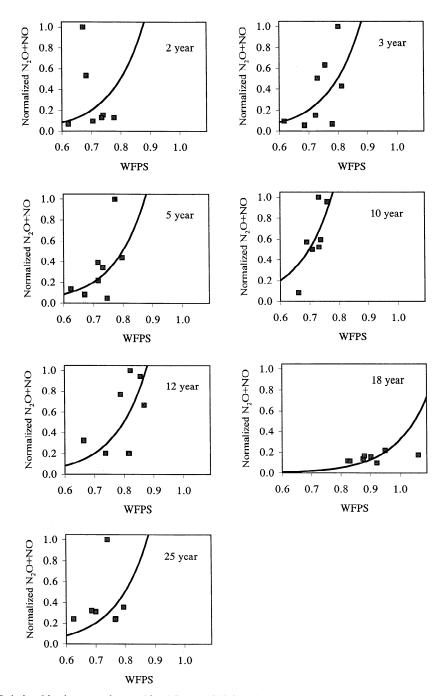


Figure 3. Relationships between the combined fluxes of N_2O and NO and WFPS along a chronosequence of pastures. Solid squares are field measurements [Keller et al., 1993]. Lines are predictions based on the relationship found in the primary forests [Keller and Reiners, 1994; Liu et al., submitted manuscript, 1999] adjusted by the shift1 factor.

Equations (5) and (7) can be reorganized as

$$F_p = 0.00085 \ e^{9.13 \ (Wp - \Delta W + \text{shift1})}$$
 (8)

$$(N_2O:NO)_p = 4.9 \times 10^{-6} e^{20.56 (Wf \cdot \Delta W + shift2)}$$
 (9)

where

$$\Delta W = W_f - W_p \tag{10}$$

From (8)-(10), it can be seen that if shift1 and shift2 are the same and equal to the difference in WFPS between the primary rain

forest and the pastures or ΔW , then the N₂O and NO partitioning models developed from the primary rain forests can be readily applied to those pastures. In fact, these three parameters are equivalent within a surprisingly narrow range of variability (Figure 5). This tendency might imply that the relationships for N₂O and NO production and the partitioning of N₂O and NO were consistent across different land use and cover systems. Some of the discrepancies between shift1, shift2, and ΔW could be caused by measurement errors in WFPS, soil bulk density, and porosity

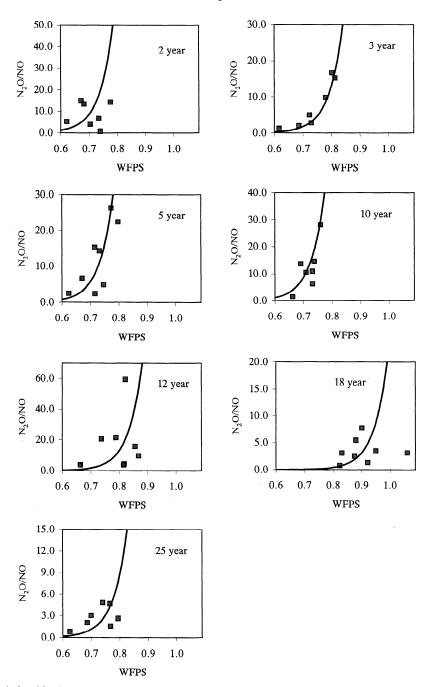


Figure 4. Relationships between N_2O and NO ratio and water-filled pore space along a chronosequence of pastures. Solid squares are field measurements [Keller et al., 1993]. Lines are predictions based on the relationship found in the primary forests [Keller and Reiners, 1994; Liu et al., submitted manuscript, 1999] adjusted by the shift2 factor.

across these sites. In this study, we will first assume that shift1, shift2, and ΔW are equal in the simulation of the chronosequence, representing the average and normal situations. Then, as a sensitivity analysis, the impact of the deviations of shift1 and shift2 from ΔW on the prediction of N₂O and NO production will be explored.

2.5. Model Calibration and Testing

The WFPS and fluxes of N_2O and NO measured from the 2- and 25-year-old pastures collected in 1992 were used to calibrate

the model. The 25-year-old pasture was selected because there is minimal impact from the antecedent forests in terms of $\rm N_2O$ and NO production after pastures have been converted for 20 years, while the 2-year-old pasture was the youngest pasture in the chronosequence and the $\rm N_2O$ and NO production was the largest among all the seven pastures observed. Field measurements taken from the other five pastures, aged at 3, 5, 10, 12, and 18 years, were used for model testing. Other parameters, including SOC, forage yield, shoot, and root biomass, observed in this area but not on those sites were also used in model calibration and testing. The

model was further tested against field measurements of N₂O and NO fluxes collected in 1996 [Veldkamp et al., 1999].

An important parameter in the simulation of total N_2O and NO emissions from soil into the atmosphere with the model is the emission coefficient (see (2)). In the simulation of N_2O and NO emissions from rain forests (Liu et al., submitted manuscript, 1999), a value of 0.042 was used. It is expected that this coefficient would have changed during the forest-pasture conversion, especially for newly converted young pastures, because site conditions, such as SOC, N availability, and bulk density, would experience significant changes. To account for the change of emission coefficient over time, we assumed that the emission coefficient decreased linearly from that of a newly derived pasture to that of a 20-year pasture:

$$a_{th} = a_c + (a_0 - a_c) m_{th}/m_c (11)$$

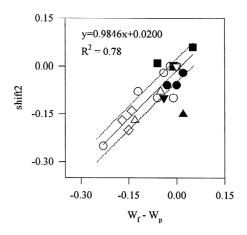
where a_{th} is the emission coefficient for the m_{th} month after clearcutting, m_c is the number of months for the system to reach quasi steady state conditions in terms of N₂O and NO production and thus a constant emission coefficient a_c . The impact of these assumptions on the emission coefficient on N₂O and NO production will be discussed using sensitivity analysis.

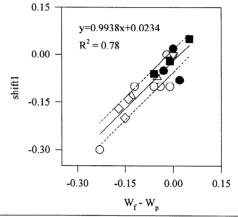
Our ability to evaluate modeling results against field measurements was limited by several factors. First, the simulation results were based on one single run at one site, representing a temporal sequence of pasture development during the first 25 years after its conversion from forest, while field measurements were taken from a chronosequence of pastures. Second, documentation about the precise initial conditions and management of these individual pastures was lacking. Actual field initial conditions were likely different than the parameterized initial conditions. Third, the climate data used to drive the model were from La Selva Biological Station, which may be different from that of Guacimo (especially the actual rainfall amount of each month), even though the long-term pattern may be similar. Fourth, the average of 4-day field measurements collected in a month was assumed to be the monthly mean. This inevitably introduced error owing to the fact that N₂O and NO emissions are greatly influenced by WFPS, which, in turn, is largely controlled by the time since the last storm occurrence before the measurements were taken. Given these limitations, our evaluation of model performance could only be based on a general representation of N₂O and NO emission patterns as measured from the chronosequences of pastures.

2.6. Model Predictions

Sensitivity analysis was performed for the following variables to investigate their impacts on N_2O and NO emissions during forest-pasture conversion: (1) emission coefficient and its temporal change; (2) amounts of ash, woody tissues, and roots left on site after slash and burn; and (3) combinations of emission coefficient, shift1, and shift2 and the amount of forest residues.

- 2.6.1. Varying emission coefficient and its representation. To investigate the significance of the assumption on the change of emission coefficient over time, we simulate the impact of several hypothetical scenarios about the emission coefficient on N_2O and NO emissions.
- 1. In case 1, the emission coefficient does not change during the first 20-year transition period of forest-pasture conversion and its value is the mean of the emission coefficients of the two pasture sites, 2 and 25 years old, used for model calibration.





- O Pasture Chronoscquence (Keller et al., 1993)
- △ Natural, Improved & Fertilized Pastures (Veldkamp et al., 1997)
- Active Pastures (Keller & Reiners, 1994)
- Abandoned Pastures (Keller & Reiners, 1994)
- Secondary Forests (Keller & Reiners, 1994)
- ▲ High Terrace Banana Plantation (Veldkamp & Keller, 1997)
- ▼ Low Terrace Banana Plantation (Veldkamp & Keller, 1997)

Figure 5. Comparison of WFPS difference between pastures and primary forests $(W_f - W_p)$ and the WFPS shifts. WFPS shifts are shown in Figure 2 and described in detail in the text. WFPS data of primary forests are from *Keller and Reiners* [1994].

2. In case 2, the emission coefficient is a function of gross N mineralization:

$$a = a_2/(1 + a_2/(N_{min} + 0.01))$$
 (12)

where a_2 is the emission coefficient of the 2-year-old pasture, which is believed to have a high gross N mineralization rate. Therefore (12) defines an emission coefficient varying between a_2 and 0.

3. In case 3, the emission coefficient is a function of bulk density or pasture age. It has been demonstrated that soil bulk density increases linearly with pasture age in this region [Stuhrmann et al., 1994; Keller et al., 1993] (Figure 6). We assume that the rate of change of bulk density with age or the slope of the linear regression in Figure 6 reflects the change of emission coefficient over time. Therefore the emission coefficient during the first 20-year transition period can be described by

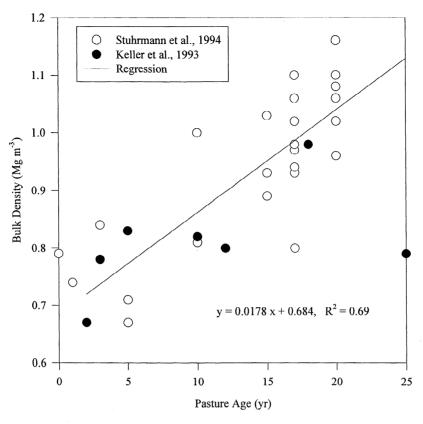


Figure 6. Soil bulk densities of forest-derived pastures.

$$a = 0.0178 (20 - pasture age) + a_{25}$$
 (13)

The first part of the right side indicates that the forcing of clear-cut on the emission coefficient disappears linearly to the age of 20 years.

2.6.2. Varying the amounts of forest residues left on site after deforestation. We consider three cases here. Case 1 is the normal input scenario. We assume, under normal conditions, all large wood has been harvested and all leaves were burned during slash and burn. In addition, only 20% of branches, 50% of the aboveground large woody debris, and 80% of the coarse and fine roots and their debris were left on site after deforestation (Table 3). Ash produced after slash and burn was estimated to be 350 gC m⁻², based on the efficiency of ash production of slash and burn at a secondary forest site in the same area [Ewel et al., 1981]. Case 2 is the low input scenario. We assume the inputs of branches, large wood and coarse roots were 30% lower than those under normal conditions and that inputs of fine roots and ash were based on Ewel et al. [1981]. Case 3 is the high input scenario. Inputs of branches, large wood, and coarse roots were 30% higher and inputs of fine roots and ash were 50% higher than those under normal conditions.

2.6.3. Testing the overall impact of forest residue addition, emission coefficient, shift1 and shift2 on N_2O and NO emissions. N_2O and NO production under various combinations of those variables was examined. The three scenarios of forest residue addition to the newly converted pasture as described above were used here. Other variations considered were emission coefficient $\pm 50\%$ around its normal values (values obtained

through calibration and testing), and shift 1 and shift 2 ± 1 standard deviation of its difference with Δ WFPS, representing the dispersion of points around the 1:1 line in Figure 5. Only three combinations that gave highest, normal and lowest predictions on N₂O and NO fluxes will be discussed. In case 1 (normal conditions), the predictions of N₂O and NO emissions are performed under normal conditions, which are the conditions calibrated from field measurements of SOC, WFPS, and N₂O and NO emission rates. In case 2 (unfavorable conditions), for N₂O production, the unfavorable conditions were low-input scenario, emission coefficient - 50%, shift1-standard deviation, and shift2standard deviation; for NO production, the unfavorable conditions were low-input scenario, emission coefficient - 50%, shift1standard deviation, and shift2+standard deviation. In case 3 (favorable conditions), for N₂O production, the favorable conditions were high-input scenario, emission coefficient + 50%, shift1+standard deviation, and shift2+standard deviation; for NO production, the favorable conditions were high-input scenario, emission coefficient + 50%, shift1+standard, and shift2-standard deviation.

3. Results

3.1. Model Calibration

The simulated monthly averages of N_2O and NO emission rates from the 2-year-old pasture were 529.2 \pm 124.2 and 68.2 \pm 17.0 mgN m⁻² month⁻¹, respectively, which were not significantly different ($\alpha = 0.05$) from field measurements of N_2O (404.4 \pm

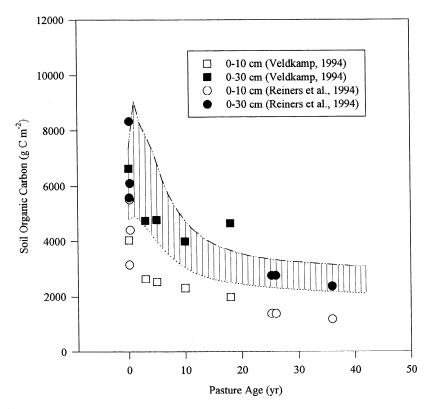


Figure 7. Comparison of simulated and observed soil organic carbon dynamics after forests being converted to pastures. The higher boundary of prediction was based on the high input scenario of forest residue (see text for details) with a passive soil organic carbon (SOC) pool size of 3000 g C m² [Veldkamp, 1994], and the lower boundary of prediction was based on the low-input scenario of forest residue with a passive SOC pool size of 2300 g C m² [Veldkamp, 1994].

195.0 mgN m² month¹) and NO (71.9 \pm 20.9 mgN m² month¹). The emission coefficient of the soil was calibrated to be 0.35, which was about 8 times the emission coefficient of the rain forests (Liu et al., submitted manuscript, 1999). The simulated N₂O and NO fluxes also agreed well with field measurements on the 25-year-old pasture. The emission coefficient of the 25-year-old pasture soil was calibrated to be 0.05, which was close to that of the rain forests (Liu et al., submitted manuscript, 1999).

For the calibration of an ecosystem model, it is necessary to compare model outputs with measurements of multiple variables to make sure that the whole ecosystem behavior is predicted reasonably well. In our simulation, the predicted monthly average carbon contents in the above- and belowground biomass were 318 and 113 gC m⁻² for the 2-year-old and 84 and 365 gC m⁻² for the 25-year-old pasture, respectively. The simulated annual aboveand belowground production values were 620 and 80 gC m⁻² yr⁻¹ for the 2-year-old and 306 and 40 gC m⁻² yr⁻¹ for the 25-year-old pasture, respectively. The total primary production of the 25-yearold pasture (346 gC m⁻² yr⁻¹) agreed well with 340 gC m⁻² yr⁻¹ predicted by Parton et al. [1994b, 1995] for humid pasture ecosystems. Primary production allocated to shoots was 7.5 times higher than that allocated to roots because of grazing; this was consistent with the field observations that aboveground production could be increased by frequent mowing, cutting, or grazing, which can increase the shoot/root ratio of production [Bushby et al., 1992; Turner et al., 1993; Veldkamp, 1993]. The forage yields or biomass being grazed were about 300 and 270 gC m⁻² yr⁻¹, respectively, for the 2-year-old and 25-year-old pasture and were comparable with field observations of 250 to 400 g C m⁻² yr⁻¹ (B.A.M. Bouman, personal communication, 1998).

3.2. Model Testing

The simulated SOC in the top 30 cm layer of a chronosequence of pastures agreed well with field measurements (Figure 7). The main difference between the upper and lower simulated limits of SOC in Figure 7 can largely be attributed to the difference in passive SOC, which has a very slow decomposition rate. *Veldkamp* [1994] has observed a difference of 700 g C m⁻² in passive SOC between two Inceptisol soils. The decrease of total SOC in the first 15 to 20 years was mainly caused by the decomposition of slow SOC, because the decomposition rates of fast and passive SOC were either too fast or too slow (Liu et al., submitted manuscript, 1999) to produce such a pattern of total SOC dynamics (Figure 7). Therefore slow SOC is the main source of N for N₂O and NO production during the transition period.

The model performed well in the prediction of WFPS and fluxes of N_2O and NO from the five comparison sites aged at 3, 5, 10, 12, and 18 years (Figures 8-10). The predicted annual WFPS values were not significantly different from field measurements (α =0.05). The striking difference between 1992 and 1996 is the apparent decrease in N_2O fluxes from all younger pastures (see

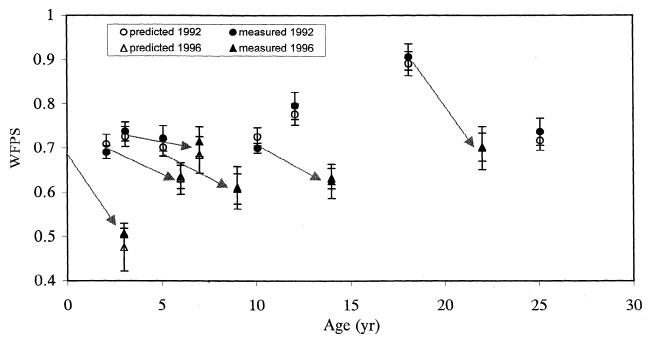


Figure 8. Comparison of predicted and measured WFPS with 1 standard error along a chronosequence of pastures. Measurements were taken in 1992 [Keller et al., 1993] and 1996 [Veldkamp et al., 1999], respectively. Arrows emphasize the changes of WFPS between those two sets of measurements.

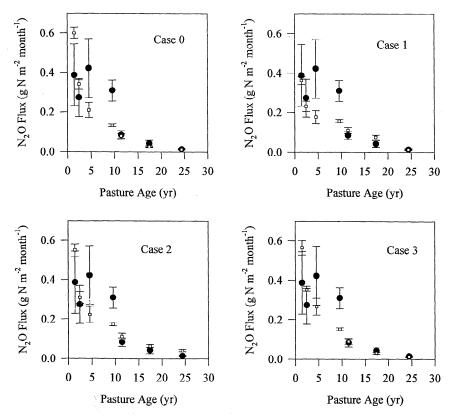


Figure 9. Comparison of predicted (open squares) and measured (solid circles) N_2O fluxes with 1 standard error along a chronosequence of pastures using different schemes of representation of the changes of emission coefficient over time. See text for detailed descriptions of these schemes. Measurements were taken in 1992 [Keller et al., 1993].

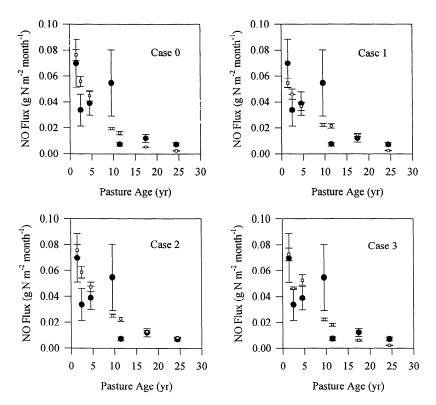


Figure 10. Comparison of predicted (open squares) and measured (solid circles) NO fluxes with 1 standard error along a pasture chronosequence using different schemes of representation of the changes of emission coefficient over time. See text for details. Measurements were taken in 1992 [Keller et al., 1993].

Figures 9 and 11), which was qualitatively attributed to the lower WFPS in 1996 compared to 1992 [Veldkamp et al., 1999] (see Figure 8). The model successfully predicted the different patterns of N_2O and NO fluxes as observed in 1996 (Figure 11). The average predicted fluxes of N_2O and NO during the observational period in 1996 were 0.14 \pm 0.03 (1 standard error) and 0.07 \pm 0.02 gN m² month¹, respectively, which were not significantly different from field measurements of 0.11 \pm 0.03 (N_2O) and 0.07 \pm 0.01 (NO) gN m² month¹ (α =0.05).

The predicted annual average N₂O and NO fluxes from the five test sites followed the general pattern of N₂O and NO fluxes as measured in the field (case 0 in Figures 9 and 10). This supports our proposition that the emission coefficient of the soil for N₂O and NO emissions decreases linearly from 0.35 as the pasture becomes older until the age of 20 years, when the emission coefficient reaches a constant of 0.05.

Predicted N_2O and NO fluxes demonstrated strong opposite seasonal patterns; N_2O fluxes were higher in the wet season, while NO fluxes were lower (Figure 12). Although field measurements were scattered between the extremes of predicted fluxes, there were no apparent seasonal patterns, especially for NO fluxes. The lack of apparent seasonal pattern in field measurements may be caused by (1) a weaker $N_2O:NO$ — WFPS relationship in the pastures (Figure 4) than in primary rain forests (Liu et al., submitted manuscript, 1999) because of other factors having a stronger impact on $N_2O:NO$ ratio than in the primary forest or (2) the sample sizes (eight for N_2O and four for NO) might not be large enough to catch a possibly higher spatial variability of N_2O

and NO fluxes at these sites than in the primary forest. Luizao et al. [1989] found strong seasonal patterns in N_2O emissions from pastures near Manaus, Brazil. Other controlling factors, including soil, climate, and management methods, might have caused these kinds of regional differences. More field data are needed in order to better understand the phenomenon and construct models at a more fundamental level.

3.3. Model Predictions

3.3.1. Temporal change of emission coefficient. Simulation results indicated that a mean invariant emission coefficient for the whole transition period could not produce the magnitude of change in N_2O and NO emissions as measured in the field (case 1 in Figures 9 and 10): fluxes from 1- to 10-year-old pastures were underestimated, while fluxes from 10- to 20-year-old pastures were overestimated. This meant that gross N mineralization rate declined more slowly over time than did N_2O and NO emissions. There was no significant difference among the other three schemes (case 0, which was based on (11), case 2, and case 3) used to represent the temporal change of the emission coefficient. However, both case 0 and case 3 depended on the assumption that the forcing of clear-cut on trace gas emissions decreases linearly with age.

3.3.2. Forest residue addition. Uncertainties of model simulation of N₂O and NO emissions from soil into the atmosphere could be introduced by the initial conditions of the site (such as total organic carbon in the soil, soil bulk density, and porosity), amounts of C and N returned to the site after clear-cutting, slash

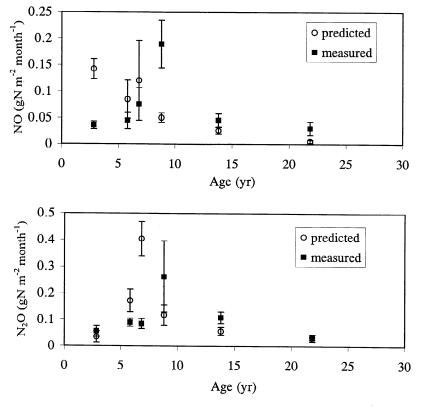


Figure 11. Comparison of measured and predicted N₂O and NO fluxes with 1 standard error along a pasture chronosequence. Measurements were taken in 1996 [Veldkamp et al., 1999] on the same chronosequence as established by Keller et al. [1993].

and burn, and other management practices such as grazing. In this section, we look at the effects of the amounts of forest residues left on the newly derived pasture on the net increase of total N_2O and NO production.

Under the normal scenario, forest-pasture conversion caused an initial increase of about 463 kg N₂O-N ha⁻¹ and 51 kg NO-N ha⁻¹ trace gas emissions from the site (Table 3) compared to the emission rate from primary rain forests (Liu et al., submitted manuscript, 1999). Nitrous oxide emission rates from pastures during the first 16 years were higher than those from its precedent primary forest and then declined to levels lower than forest soil emissions assuming no use of fertilizers at the pasture (Figure 12), consistent with the field measurements [Keller et al., 1993]. In contrast, the increase of nitric oxide only lasted about 11 years after deforestation. N₂O-N comprised 90% of the nitrogen loss through increased N₂O and NO emissions, while NO-N accounted for only 10%.

If forest residue left on site followed the low scenario, the simulated net increase in total N_2O and NO production from the site would be 360 kg N_2O -N ha⁻¹ and 41 kg NO-N ha⁻¹, a 22% reduction in N_2O -N emission and 20% reduction in NO-N emission compared to the normal scenario of organic matter addition (Table 3). However, there was little change in the length of time when the net increase happened, compared to the normal scenario. No change was found in the composition of the increased nitrogen gases; N_2O -N = 90% and NO-N = 10% of the total N.

Under the scenario with high input of forest residue, the

simulated net increase of total N_2O and NO production was 494 kg N_2O -N ha⁻¹ and 54 kg NO-N ha⁻¹ compared to that from the precedent primary forests, and the increase lasted about 18 years (Table 3). The addition of 30-50% of forest residue to the normal scenario only led to an increase of 7% in total nitrogen loss through N_2O and NO emissions from the system during the transition period. No change was found with respect to the species composition of N_2O and NO.

3.3.3. Combinations of environmental conditions on N2O and NO emissions. Under favorable conditions for N2O emissions (high-input scenario, emission coefficient +50%, shift1 + standard deviation, shift2+standard deviation), N2O emission rates from the derived pasture were higher than those from rain forest in the first 18 years, which led to an increased emission of 668 kgN ha⁻¹ during this period (Table 4). Under unfavorable conditions (lowinput scenario, emission coefficient-50%, shift1-standard deviation, shift2-standard deviation), the increase of N₂O emissions only occurred in the first 13 years and the net increase was only 150 kgN ha⁻¹. Under favorable conditions (high-input scenario, emission coefficient + 50%, shift1 + standard deviation, shift2 standard deviation), the increase of NO emissions caused by forestpasture conversion lasted for about 16 years and the cumulative net increase of NO was 177 kgN ha⁻¹. In contrast, under unfavorable conditions (low-input scenario, emission coefficient-50%, shift1standard deviation, shift2+standard deviation), the increase of NO emissions occurred only in the first 3 years and the cumulative net increase during this period was only 8 kgN ha-1. On the basis of

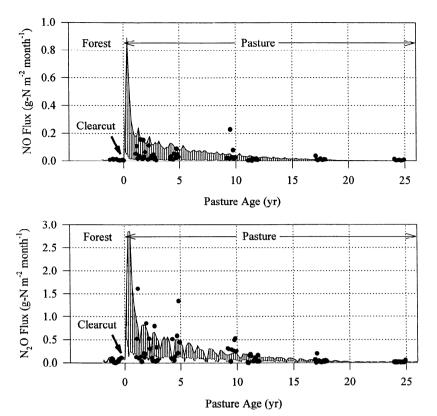


Figure 12. Comparison of measured and predicted temporal variations of N₂O and NO emission rates from soils into the atmosphere following the conversion of a primary forest to pasture under various scenarios. Top boundary of prediction was based on high-input scenario of forest residue, emission coefficient+50%, shift1+standard deviation and shift2+standard deviation for N₂O fluxes; high-input scenario of forest residue, emission coefficient+50%, shift1+standard deviation and shift2-standard deviation for NO fluxes. Bottom boundary of prediction was based on low-input scenario of forest residue, emission coefficient-50%, shift1-standard deviation and shift2-standard deviation for N₂O fluxes; low-input scenario of forest residue, emission coefficient-50%, shift1-standard deviation and shift2+standard deviation for NO fluxes. Solid circles are field measurements taken from different sites [Keller et al., 1993].

the previous analysis, it can be seen that N₂O and NO emissions from forest-derived pastures are very sensitive to forest residue input, emission coefficient, and shift1 and shift2.

4. Discussion

In this study, we propose to use emission coefficients of N_2O and NO from soil into the atmosphere to characterize both the efficiency of N_2O and NO production in terms of N cycling rate (gross N mineralization) in the soil and the N_2O and NO diffusion coefficient between the production site and the atmosphere. We believe that the emission coefficient depends on several factors, e.g., N availability, site of production of N_2O and NO in the soil profile, soil texture, and WFPS. Therefore the emission coefficient is conceptually in agreement with the "hole-in-the-pipe" model as formalized by *Davidson* [1991] to represent the N_2O formation in and emission from soils. More field studies are required to relate the emission coefficient to its controlling factors.

The scaling method for the N_2O+NO — WFPS and $N_2O:NO$ — WFPS relationships found in various ecosystems is effective. The statistical equivalency of WFPS between two sites and shift1 and shift2 is important to regional or even global simulations of N_2O and NO emissions from various ecosystems (Figure 5). The

factors underlying the equivalency may lead to further understanding of the emission processes of N_2O and NO from various ecosystems in a region, although we are not prepared to suggest which factors could be used to explain these results, at present. Nevertheless, we can see several points from these generalized relationships:

- 1. The mathematical equations describing the N_2O+NO WFPS and $N_2O:NO$ WFPS relationships found from primary rain forests (Liu et al., submitted manuscript, 1999) are general for various land use systems. This generality is the basis for the successful scaling of those relationships across ecosystems.
- 2. The measurements obtained from primary forests can be used as the basis for comparison and scaling across ecosystems. On the basis of the general relationships (Figure 5), it can be seen that we can also use measurements obtained from any other ecosystems as the basis for scaling and comparison, and the general relationships would not change.
- 3. The magnitude of the long-term average of WFPS is not important to the emissions of N_2O and NO emissions from soil into the atmosphere, at least in the humid tropical zone of Costa Rica. Although some ecosystems demonstrated 20% difference in their long-term mean WFPS, they demonstrated similar N_2O+NO WFPS and $N_2O:NO$ WFPS relationships, if the WFPS

Table 4. Impact of Environmental Conditions on the Emissions of N_2O and NO From a Chronosequence of Pastures

Conditions	Net Increase, kgN ha ⁻¹		Years of Increase, years	
	N ₂ O	NO	N ₂ O	NO
Unfavorable	150	8	13	3
Normal	463	51	16	12
Favorable	668	177	18	16

Net increase is calculated as the cumulative difference of N_2O and NO emissions between pastures and primary forests during the period with positive net increase. See text for the explanation of the normal, favorable, and unfavorable conditions for N_2O and NO production.

difference were eliminated (Figure 5). This may further indicate that microbial populations could easily adapt to their environmental conditions, especially high WFPS. Of course, error in WFPS could be introduced by field measurements of gravimetric water contents, bulk density, and the assumption that particle density is 2.65 Mg m⁻³.

4. The scatter of points around the regression lines in Figure 5 has important implications for the variabilities of the $N_2O+NO-WFPS$ and $N_2O:NO-WFPS$ relationships found in various ecosystems. A small deviation of a point from the regression line may indicate a large change in the $N_2O+NO-WFPS$ or $N_2O:NO-WFPS$ relationship, because the small deviation in the exponent represents a corresponding larger change in the relationships (see Eq. (5)). As a result, the total fluxes of N_2O and NO and the partitioning of them may be quite different from one site to another. The degree of scatter of points around the line indicates the magnitude of variation of the $N_2O+NO-WFPS$ and $N_2O:NO-WFPS$ relationships across ecosystems, which is very useful for the simulation of regional N_2O and NO fluxes. We will discuss this issue in a separate paper.

All the simulated results presented above indicate that the impacts of forest-pasture conversion on N₂O and NO emissions from soil into the atmosphere are complex. They depend on the initial conditions of the derived pastures, management practices, soil physiochemical and biological properties, N availability, and climate. This variability has been documented by the limited N₂O and NO field measurements in the tropics [e.g., Luizao et al., 1989; Keller et al., 1993; Keller and Reiners, 1994; Keller et al., 1997]. The soil N₂O and NO emissions from pastures along two chronosequences in Brazil [Keller et al., 1997] showed that fluxes either decreased or increased compared to forests. In addition, the magnitude of increases, when they occurred, were not as pronounced as those found in Costa Rica [Keller et al., 1993]. Keller et al. [1993] and Veldkamp et al. [1999] found quite different patterns of N₂O and NO fluxes along the same pasture chronosequence. While N₂O and NO emissions from young pastures were generally greater than emissions from older pastures or forests, Veldkamp et al. [1999] did not observe consistently higher fluxes as they did in 1992. They attributed this difference to the lower WFPS observed in 1996 (Figure 8). The modified CENTURY model emphasizes the impacts of WFPS on N₂O and NO emissions from soils into the atmosphere and has successfully predicted the patterns of N_2O and NO observed in both 1992 and 1996. That the N_2O emission rates from old pastures were sometimes higher than in the primary forests (see *Luizao et al.* [1989] and *Keller et al.* [1997]) probably depended on soil type and pasture management practices. It is possible that N_2O and NO emissions would have demonstrated a slightly different pattern, especially the seasonal pattern, if the field measurements were taken in more than 1 year.

5. Summary

Field measurements indicated that N_2O and NO emissions from a chronosequence of pastures were higher than those from primary rain forests in the first 15 years after being converted from forests and then declined to levels less than those from the precedent primary forests [Keller et al., 1993]. The modified CENTURY model has been successfully extended to simulate this general trend through the chronosequence of pastures. The model assumes that the emission coefficient of pasture soils in terms of N_2O and NO emissions decreases linearly until the age of 20 years and then reaches a constant emission coefficient. This assumption is supported by a parallel increase of soil bulk density during the same period.

The general relationships between N_{N_2O-NO} , the ratio of N_2O to NO, and ΔW for various land use systems with different land management history presented in this paper suggest a useful and convenient way to scale up N_2O and NO fluxes from sites to regions. The N_2O and NO emitted from soils are proportional to the gross N mineralization rate. The magnitude of this proportion or emission coefficient may be dependent on factors such as the distance between the production site of nitrogen gases and the soil-atmosphere interface. Finding the biogeochemical and physical bases of the emission coefficient would be very helpful for the prediction of total N_2O and NO emissions from areas where no field measurements have been taken.

The combined flux of N_2O and NO increases exponentially with WFPS to its maximum at the monthly timescale. Although WFPS varies from site to site and from ecosystem to ecosystem, this relationship is general across various land use systems, including primary and secondary forests, active and abandoned pastures, and banana plantations. The $N_2O+NO-W_f$ relationship developed from the primary rain forest can be extended to other land use systems without any modification of the parameters because the scaling factor shift1 for the $N_2O+NO-W_p$ relationship and ΔW between the forest and any pasture was statistically equivalent (Figure 5).

The N₂O:NO ratio increases exponentially with WFPS. This relationship is consistent across various land use systems (Figure 4). The N₂O:NO — W_f relationship developed from the primary rain forest (Liu et al., submitted manuscript, 1999) can also be extended to other land use systems without any modification of the parameters because the scaling factor shift2 for the N₂O:NO — W_p relationship and ΔW between the forest and any pasture was statistically equivalent (Figure 5), and the difference, if any, might be caused by observational errors in WFPS, soil bulk density, and porosity.

Field measurements collected in different regions show different impacts of forest to pasture conversions on N₂O and NO emissions (see *Luizao et al.* [1989], *Keller et al.* [1993] and *Keller et al.* [1997]), depending on soil, climate, and management practices of the pastures. Although it is more feasible to examine the change

of N₂O and NO emissions using the chronosequence method, it would be preferable to compare measurements on a single site over time. Such long-term measurements can only rarely be made, however, so that, practically speaking, a well-selected chronosequence is the most likely means of understanding trends in phenomena such as changes in trace gas emissions over time.

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References

- Bouwman, A. F., K. W. Van der Hoek, and J. G. J. Olivier, Uncertainties in the global source distribution of nitrous oxide, J. Geophys. Res., 100, 2785-2800, 1995.
- Bushby, H. V. A., I. Vallis, and R. J. K. Myers, Dynamics of C in a pasture grass (Panicum maximum var. Trichoglume)-soil system, *Soil Biol. Biochem.*, 24, 381-387, 1992.
- Crutzen, P.J., The influence of nitrogen oxides on the atmospheric ozone content, Q. J. R. Meterol. Soc., 96, 320-325, 1970.
- Davidson, E.A., Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems, in *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes*, edited by J. E. Rogers and W. B. Whitman, pp. 219-235, Am. Soc. for Microbiol., Washington, D.C., 1991.
- Eklund, T. J., W. H. McDowell, and C.M. Pringle, Seasonal variation of tropical precipitation chemistry: La Selva, Costa Rica, Atmos. Environ., 31, 3903-3910, 1997.
- Ewel, J., C. Berish, B. Brown, N. Price, and J. Raich, Slash and burn impacts on a Costa Rican wet forest site. *Ecolology*, 62, 816-829, 1981.
- Firestone, M. K., and E. A. Davidson, Microbiological basis of NO and NO production and consumption in soil, in *Exchange of Trace Gases Between Terrestrial Ecosystems and the Atmosphere*, edited by M. O. Andreae and D. S. Schimel, pp. 7-21, John Wiley, New York, 1989.
- Harmon, M. E., et al., Ecology of coarse woody debris in temperate ecosystems, Adv. Ecol. Res., 15, 133-302, 1986.
- Ibrahim, M. A., Compatibility, persistence and productivity of grasslegume mixtures for sustainable animal production in the Atlantic Zone of Costa Rica, Ph. D. thesis, Univ. of Wageningen, Wageningen, Netherlands, 1994.
- Keller, M., and P. A. Matson, Biosphere-atmosphere exchange of trace gases in the tropics: Evaluating the effects of land use changes, in Global Atmospheric-Biospheric Chemistry, edited by R. G. Prinn, pp. 103-117, Plenum, New York, 1994.
- Keller, M., and W. A. Reiners, Soil-atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica, Global Biogeochem. Cycles, 8, 399-409, 1994.
- Keller, M., E. Veldkamp, A. M. Weitz, and W. A. Reiners, Effect of pasture age on soil trace-gas emissions from a deforested area of Costa Rica, *Nature*, 365, 244-246, 1993.
- Keller, M., J. Melillo, and W. A. Mello, Trace gas emissions from ecosystems of the Amazon basin, J. Braz. Assoc. Adv. Sci., 49, 87-97, 1997
- Lugo, A. E., Management of tropical biodiversity, *Ecol. Appl.*, 5, 956-961, 1995
- Lugo, A. E., J. A. Parrotta, and S. Brown, Loss in species caused by tropical deforestation and their recovery through management, *Ambio*, 22, 106-109, 1993.
- Luizao, F., P. A. Matson, G. Livingston, R. Luizao, and P. M. Vitousek, Nitrous oxide flux following tropical land clearing, Global Biogeochem. Cycles, 3: 281-285, 1989.
- McElroy, M. B., and J. C. McConnel. Nitrous oxide: A natural source of stratospheric NO, *J. Atmos. Sci.*, 28, 1095-1098, 1971.
- Nevison, C., and E. Holland, A reexamination of the impact of anthropogenically fixed nitrogen on atmospheric N₂O and the stratospheric O₃ layer, J. Geophys. Res., 102, 25,519-25,536, 1997.

- Parsons, W. F. J., and M. Keller, Controls on nitrate oxide emissions from tropical pasture and rain forest soils, *Biol. Fertil. Soils*, 20, 151-156, 1995.
- Parsons, W. F. J., M. E. Mitre, M. Keller, and W. A. Reiners, Nitrate limitation of N₂O production and denitrification from tropical pasture and rain forest soils, *Biogeochem.*, 22, 179-193, 1993.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima, Analysis of factors controlling soil organic matter levels in Great Plains grasslands, Soil Sci. Soc. Am. J., 51, 1173-1179, 1987.
- Parton, W. J., et al., Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide, Global Biogeochem. Cycles, 7, 785-809, 1993.
- Parton, W. J., D. S. Ojima, C. V. Cole, and D. S. Schimel, A general model for soil organic matter dynamics: Sensitivity to litter chemistry, texture and management, in *Quantitative Modeling of Soil Forming Processes*, SSSA Spec. Publ. 39, pp. 147-167, Madison, Wisc., 1994a.
- Parton, W. J., D. S. Ojima, C. V. Cole, and D. S. Schimel, Environmental change in grasslands: Assessment using models, *Climate Change*, 28, 111-141, 1994b.
- Parton, W. J., J. M. O. Scurlock, D. S. Ojima, D. S. Schimel, D. O. Hall, and SCOPEGRAM Group Members, Impact of climate change on grassland production and soil carbon worldwide, *Global Change Biol.*, 1, 13-22, 1995.
- Phillips, O. L., The changing ecology of tropical forests, *Biodiversity Conserv.*, 6, 291-311, 1997.
- Prinn, R., D. Cunnold, R. Rasmussen, P. Simmonds, F. Alyea, A. Crawford, P. Fraser, and R. Rosen, Atmospheric emissions and trends of nitrous oxide deduced from 10 years of ALE-GAGE data, *J. Geophys. Res.*, 95, 18,369-18,385, 1990.
- Reiners, W. A., A. F. Bouwman, W. F. J. Parsons, and M. Keller, Tropical rain forest conversion to pasture: Changes in vegetation and soil properties, *Ecol. Appl.*, 4, 363-377, 1994.
- SAS Institute Inc., SAS/STAT User's Guide, version 6, 4th ed., Cary, N.C., 1990.
- Schimel, D. S., B. H. Braswell, and W. J. Parton, Equilibration of the terrestrial water, nitrogen, and carbon cycles, *Proc. Natl. Acad. Sci.* U. S. A., 94, 8280-8283, 1997.
- Stuhrmann, M., C. Bergmann, and W. Zech, Mineral nutrition, soil factors and growth rates of Gmelina arborea plantations in the humid lowlands of northern Costa Rica, For. Ecol. Manage., 70, 135-145, 1994.
- Turner, C. L., T. R. Seastedt, and M. I. Dyer, Maximization of aboveground grassland production: The role of defoliation frequency, intensity and history, *Ecol. Appl.*, 3, 175-186, 1993.
- Veldkamp, E., Soil organic carbon dynamics in pastures established after deforestation in the humid tropics of Costa Rica, Ph. D. thesis, 117 pp., Univ. of Wageningen, Wageningen, Netherlands, 1993.
- Veldkamp, E., Organic carbon turnover in three tropical soils under pasture after deforestation, Soil Sci. Soc. Am. J., 58, 175-180, 1994.
- Veldkamp, E., and M. Keller, Nitrogen oxide emissions from a banana plantation in the humid tropics, J. Geophys. Res., 102, 15,889-15,898, 1997.
- Veldkamp, E., M. Keller, and M. Nunez, Effects of pasture management on N₂O and NO emissions from soils in the humid tropics of Costa Rica, Global Biogeochem. Cycles, 12, 71-79, 1997.
- Veldkamp, E., E. Davidson, H. Erickson, and M. Keller, 1999. Soil nitrogen cycling and nitrogen oxide emissions along a pasture chronosequence in the humid tropics of Costa Rica, Soil Biol. Biochem, in press, 1999.
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